

- IX. "Summary of the principal Results obtained in a Study of the Development of the Tuatara (*Sphenodon punctatum*).” By Professor A. DENDY. Communicated by Professor HOWES, F.R.S.

- X. "Tables for the Solution of the Equation

$$\frac{d^2y}{dx^2} + \frac{1}{x} \frac{dy}{dx} - \left(1 + \frac{h^2}{x^2}\right)y = 0."$$

By W. STEADMAN ALDIS, M.A. Communicated by J. J. THOMSON, F.R.S.

- XI. "The Stomodæum, Mesenterial Filaments, and Endoderm of *Xenia*." By J. H. ASHWORTH, B.Sc. Communicated by Professor HICKSON, F.R.S.

The Society adjourned over the Long Vacation to Thursday, November 17th, 1898.

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"Observations on Stomata." By FRANCIS DARWIN, F.R.S.  
Received May 31,—Read June 16, 1898.

(Abstract.)

The method described depends on the fact that in adult leaves transpiration is stomatal rather than cuticular, so that, other things being equal, the yield of watery vapour depends on the degree to which the stomata are open, and may be used as an index of their condition. In principle, it is the same as the methods of Merget\* and Stahl.† These observers used hygroscopic papers impregnated with reagents which change colour according as they are dry or damp, and Stahl, who employed paper soaked in cobalt chloride, has obtained excellent results. In my laboratory I have used, for some years, a hygroscope for demonstrating stomatal transpiration, in which evaporation is indicated by the untwisting of the awn of *Stipa pennata*;‡ my present instrument is of the same general type, but the index is made of "chinese leaf," i.e., shavings of pressed and heated horn.§ If a strip of horn is placed on a dry substance, e.g., the astomatal surface of a leaf, it does not move, but on the stomatal surface, it instantly curves strongly away from the transpiring surface. In the hygroscope the

\* 'Comptes Rendus,' 1878.

† 'Bot. Zeitung,' 1894.

‡ Darwin and Acton, 'Practical Physiology of Plants,' 1st edition, 1894.

§ I also use the epidermis of a *Yucca*—a material which I owe to the kindness of Mr. Thiselton-Dyer.

degree of curvature is read off on a graduated quadrant, and in this way a numerical indication of the condition of the stomata is obtained.

The instrument makes no claim to accuracy, but has proved extremely useful when used comparatively to indicate and localise small changes in the transpiration of leaves, and therefore by implication, changes in the condition of the stomata. By observing under the microscope the uninjured leaf of *Caltha palustris*, and comparing the variations in the size of the stomata with the variations in the readings of the hygroscope, it is easy to convince one's self of the value of the method. It must be especially noted that though a fall in the hygroscope readings corresponds with a narrowing of the stomatal opening, it does not follow that zero on the hygroscopic scale means absolute closure of the stomata. This want of sensitiveness has one advantage, namely, that cuticular transpiration has no effect on the horn index, so that any movement of the index must depend on a stomatal transpiration. The hygroscope indicates well the gradual "closure"\* of the stomata that occurs as a plucked leaf withers. It is generally stated that marsh and aquatic plants do not close their stomata under these circumstances. I find that, although the phenomenon is much less marked than in terrestrial plants, yet that, in many species, partial closure of the stomata undoubtedly occurs in the aquatic class.

The most interesting fact observed in withering leaves is that in many cases the "closure" of the stoma is preceded by temporary opening, which may occur almost simultaneously with the severance of the leaf from the plant. Thus the hygroscope readings rise at first, and subsequently sink to zero. The interest of this fact is the demonstration of the interaction between the guard cells and the surrounding epidermis. The phenomenon is best seen in plants with milky juice, but is not confined to this class. The preliminary opening of the stomata occurs in the early morning, but not in the evening—a fact which is of importance in relation to the mechanism of the nocturnal closure of the stomata.

A diminution of the stomatal transpiration can also be brought about by compressing the stem of the plant in a vice, a process which is known to diminish the water supply.† The stomatal closure is here probably an adaptive response to the lowering of the water-supply of the leaf, but this is not quite certain.

A series of experiments were made on the comparative effect of moist and dry air, from which it is clear that the stomata "close" before any visible signs of flaccidity occur in the leaf. When leaves are exposed to air dried by  $\text{H}_2\text{SO}_4$ , "closure" is preceded by a remark-

\* I use the word "closure" to mean such a narrowing of the stomatal aperture as corresponds with zero on the hygroscope.

† F. Darwin and R. Phillips, 'Camb. Phil. Soc. Proc.', 1886.

ably prolonged opening of the stomata—a phenomenon which requires further investigation.

Baranetzky\* showed that slight degrees of disturbance affect transpiration. The hygroscopic gives no evidence of increased transpiration when the disturbance is slight. When the plant is violently shaken the leaves become flaccid and the stomata “close,” and in some cases the closure is preceded by increased transpiration, no doubt due to temporary opening of the stomata, induced by the guard cells being released from epidermal pressure before they have lost their own turgor.

N. J. C. Müllert† showed that stomata may be closed by electric stimulation; my experiments show that while a strong shock narrows the stomata, a weaker one opens them, no doubt owing to the temporary loss of epidermal pressure.

Some experiments on poisonous gases and vapours were made. Chloroform and ether slowly “close” the stomata, which finally reopen in a normal atmosphere. Pure CO<sub>2</sub> also slowly closes the stomata.

The hygroscopic is well fitted to demonstrate the fundamental facts in relation to light. The fact that the stomata are widely open in sunshine is well known; the difference between bright and less bright diffused light is not so well known, nor the fact that in dark stormy weather the stomata may be nearly closed by day, even in summer. The effect of difference of illumination is well shown in certain leaves having stomata in both surfaces, *e.g.*, *Iris*, *Narcissus*, and the phyllodes of *Acacia cyclopis*. In these the stomata on the illuminated surfaces are much wider open than on the less brightly illuminated sides; and when the plant is reversed in position in regard to light, the stomata rapidly accommodate themselves to the change in illumination.

The most interesting fact in regard to the effect of artificial darkness is that it is more effectual in producing closure in the afternoon than in the morning; and, conversely, illumination opens closed stomata more readily in the morning than later in the day. These, together with other observations, tend to show a certain amount of inherent periodicity in the nocturnal closure of the stomata. Another fact of interest is that in darkness prolonged for several days the stomata gradually open. This last observation is used in the section on the mechanism of the stoma as an argument against the prevalent view that the stoma closes in darkness, because in the abeyance of assimilation the osmotic material, on which the turgor of the guard cells depends, ceases to be manufactured.

\* ‘Bot. Zeitung,’ 1872.

† Pringsheim’s ‘Jahrbücher,’ vol. 8, 1872.

Schellenberger\* has striven to uphold this view by showing that in the absence of  $\text{CO}_2$  the stomata close as though they were in darkness. My experiments on plants deprived of  $\text{CO}_2$  lead to absolutely contrary results, namely, that the stomata remain perfectly open even during prolonged deprivation of  $\text{CO}_2$ .

It is a vexed question† whether or no the majority of plants close their stomata at night. My conclusion is that in terrestrial plants (excluding nyctitropic plants) a great majority show some closure at night; the horn hygroscopic stands at zero on the stomatal surface of by far the greater number of ordinary plants. On the other hand, the hygroscopic shows widely open stomata on most aquatic plants at night. Stahl‡ concludes that nyctitropic plants are remarkable for not closing the stomata at night; this fact I somewhat doubtfully confirm; but the question is not so simple as it seems, owing to the varying behaviour of the stomata at night in different temperatures.

Since the hygroscopic gives numerical readings, it is possible to represent graphically the daily opening and closing of the stomata. The curve begins to leave the zero with the morning light; it rises rapidly at first, and afterwards more slowly. In some cases it runs roughly horizontally until a rapid fall begins in the evening. In other cases there is a slow rise up to the highest point, which occurs between 11 A.M. and 3 P.M. The hygroscopic generally sinks to zero within an hour after sunset.

The effect of heat has not been fully studied, but enough has been done to confirm previous observers who find that heat opens the stomata. As regards the visible spectrum, I find that the red rays are decidedly most efficient, but I am not able to find any evidence of a secondary maximum in the blue, such as Kohl§ describes.

The biology of the nocturnal closure is a subject which can hardly be discussed in a condensed manner. It is suggested that the gaseous interchange of assimilation may require widely open stomata, whereas respiration may be carried on with comparatively closed apertures. If this is so, the stomata might be to a great extent shut at night, and an economy in the use of water effected, without detriment to metabolism. Observations are given to show that quite another effect is brought about by nocturnal closure. As long as the stomata are open, the transpiring leaf is considerably cooler than the dry-bulb thermometer, but at night it has almost the temperature of the air. In this way a saving of heat is undoubtedly effected—but it is not easy to say whether it is sufficient to be of much

\* ‘Bot. Zeitung,’ 1896.

† Leitgeb, ‘Mittheilungen aus dem Bot. Inst. zu Graz,’ 1886.

‡ ‘Bot. Zeitung,’ 1897.

§ ‘Beiblatt zur Leopoldina,’ 1895.

practical importance to the plant. I am inclined to believe, from Sachs'\* experiments on the depletion of leaves, that all saving of heat must be valuable, by preventing the checking of translocation which he observed on cold nights.

The mechanism of the stoma is another subject which does not lend itself to condensed treatment. I have tried to point out that the stoma has been neglected in the modern reorganisation of plant physiology from the point of view of irritability. Some observers insist on the preponderant influence of the guard cells, while Leitgeb in the same way exaggerated the importance of epidermic pressure, whereas the two factors should, as far as possible, be considered as parts of a whole and as correlated rather than opposed in action. I have also attempted to show how the stoma, like other parts of the plant, may be supposed to react adaptively to those signals, which we usually call stimuli. The attempt which I have made to rank the problem among the phenomena of irritability, is very tentative in character. I have ventured to put it forth because I am convinced that it is in this direction that advances will be made.

“Mathematical Contributions to the Theory of Evolution. V.  
On the Reconstruction of the Stature of Prehistoric Races.”  
By KARL PEARSON, F.R.S., University College, London.  
Received June 6,—Read June 16, 1898.

(Abstract).

1. The object of this memoir is to illustrate the general theory by which we may reconstruct from the knowledge of one organ in a fossil or prehistoric race, the dimensions of other organs, when the correlation between organs in existing races of the same species has been ascertained. The particular illustration chosen is the reconstruction of probable stature from a measurement of the long bones.

Up till quite recently this subject remained in great obscurity, partly on account of absence of theory, and partly for want of trustworthy data.

2. The estimated statures as obtained by Orfila, Topinard or Beddoe, or by use of their methods, differ widely, and those methods have no satisfactory theoretical basis. It was usual to suppose that there was some mean or average ratio of stature to long bone, and even when it was recognised that this ratio varied with the length of the long bone, it was thought sufficient to determine it for two or three separate ranges of stature, and determine its mean value for these ranges by a very limited number of cases.

\* ‘Arbeiten,’ 1884.